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Vegetation diversity of *Pinus pinaster* forests in the Italian Peninsula

Dario Ciaramella[1*], Martina Marei Viti[2,3*], Marco Landi[4], Kryštof Chytrý[5,6], Claudia Angiolini[1,7], Gianmaria Bonari[1,7]

1 *Department of Life Sciences, University of Siena, Siena, Italy*
2 *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany*
3 *Institute of Biology, Martin-Luther-University Halle-Wittenberg, Halle, Germany*
4 *Reparto Carabinieri Biodiversità di Siena, Siena, Italy*
5 *Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria*
6 *Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic*
7 *NBFC, National Biodiversity Future Center, Palermo, Italy*

Corresponding author: Dario Ciaramella (dario.ciaramella93@gmail.com)

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Abstract

Aim: To revise *Pinus pinaster*-dominated communities of the Italian peninsula with special regard to central-southern Tuscany, and assess their floristic and ecological differences. **Study area:** Tuscany and Liguria regions, Italy. **Methods:** We classified 251 vegetation plots using the Two-way indicator species analysis method and we explored vegetation patterns through Principal Coordinate Analysis. We then investigated the ecology using Ecological Indicator Values. **Results:** We identified four major groups, primarily distinguished by the substrate of their stands and along a latitudinal gradient. We classified the forests in central-southern Tuscany in the association *Erico scopariae-Pinetum pinastri*. This community includes thermophilous and mesophilous species primarily distributed in the Atlantic and Western Mediterranean regions. Comparison of community means of Ecological Indicator Values revealed significant differences in soil reaction, nitrogen, moisture, and light conditions, but not in temperature, between the central-southern Tuscany forests and the other clusters. We classified the other studied forest communities on acidic substrates within the association *Erico arboreae-Pinetum pinastri*, whereas those found on ultramafic substrates were placed in the *Euphorbio ligusticae-Pinetum pinastri typus cons. propos.*, and in an informal group of secondary vegetation stands. **Conclusions:** Our analyses showed that the *Pinus pinaster*-dominated forests of central-southern Tuscany belong to the association *Erico scopariae-Pinetum pinastri* of the alliance *Genisto pilosae-Pinion pinastri* (class *Pinetea halepensis*). The presence of species of phytogeographical importance in the forest understory, underscores the high biogeographic and conservation value of these pine forests.

Taxonomic reference: Euro+Med (2024-).

Syntaxonomic reference: Mucina et al. (2016), except for the changes proposed by Bonari et al. (2021).

Abbreviations: EVC = EuroVegChecklist; ICPN = International Code of Phytosociological Nomenclature; PCoA = Principal Coordinate Analysis; TWINSPAN = Two-way indicator species analysis.

Keywords

Genisto pilosae-Pinion pinastri, Maritime pine, *Pinetea halepensis*, plant communities, vegetation classification

[*] These authors share the first authorship.

Introduction

Mediterranean thermophilous pine forests are a common vegetation type throughout the Mediterranean Basin. These forests are dominated by one of the four Mediterranean thermophilous pines (*Pinus brutia*, *P. halepensis*, *P. pinaster*, and *P. pinea*). They typically occur in extreme climatic or soil conditions, such as on exposed, warm, and dry rocky slopes, on ultramafic bedrocks, marls, dolomites, and limestones (Bonari et al. 2021). Coastal and subcoastal areas of peninsular Italy, as well as Sicily, Sardinia, and other small Mediterranean islands, are characterised by extensive pine forests. These forests occur both naturally and as old or recent plantations established for timber or other tree products. In these forests, *P. pinaster* plays a prominent role in the thermo- and meso-mediterranean belts of the northwestern Tyrrhenian sector of Liguria and Tuscany regions (Central Italy), thriving mostly on siliceous and ophiolitic substrates, often with an understory of thermophilous sclerophyllous species.

Pinus pinaster s.l. (Maritime pine) is a medium-sized tree with a west-Mediterranean Atlantic range, distributed from the Mediterranean area of southwestern Europe to the Atlantic Iberian Peninsula, France, Italy, and northwestern Africa (Barbero et al. 1998; Farjon 2017). The species has a relatively wide ecology, growing in humid and sub-humid climates within a broad range of elevations, from the sea level up to 2000 m a.s.l., and on a variety of substrates, such as schists, serpentines, sandstones, granites, and soils of volcanic origin (Abad Viñas et al. 2016; Farjon 2017; Vázquez-González et al. 2020). It often forms monospecific stands, but also mixed forest stands with *Quercus* spp. or other pines. In Italy, where it is native to Liguria, Tuscany, Sicily, and Sardinia administrative regions, it reaches its eastern native distribution limit in mainland Europe (Pignatti 2017–2019).

From a phytosociological standpoint, *P. pinaster* is an important diagnostic and dominant species of the order *Pinetalia halepensis* belonging to the class *Pinetea halepensis*, which includes all Mediterranean thermophilous pine forests. This class corresponds to the EUNIS habitat type "T3A Mediterranean lowland to submontane *Pinus* forest" and partly also to "N1G Mediterranean coniferous coastal dune forest" (Chytrý et al. 2020).

In Italy, *P. pinaster* forest communities have been studied since the 70s in terms of syntaxonomy (Brullo et al. 1977; Gianguzzi 1999; Biondi and Vagge 2015; Calvia et al. 2022a). Communities on volcanic substrates found in Pantelleria Island and northeastern Sardinia were classified into *Genisto aspalathoidis-Pinetum hamiltonii* Brullo, Di Martino et Marcenò 1977 corr. Gianguzzi 1999 and *Arbuto unedonis-Pinetum pinastri* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2022, respectively (Gianguzzi 1999; Calvia et al. 2022a). Biondi and Vagge (2015) recognised three associations (*Erico scopariae-Pinetum pinastri* Biondi et Vagge 2015, *Erico arboreae-Pinetum pinastri* Biondi et Vagge 2015, and *Buxo sempervirentis-Pinetum pinastri* Biondi et Vagge 2015) distributed in western peninsular Italy, mainly related to acidic substrates with low nutrient content in coastal and inland areas of Liguria and Tuscany regions, currently attributed to the Ligurian and Provençal alliance *Genisto pilosae-Pinion pinastri* of the order *Pinetalia halepensis* (Preislerová et al. 2022). The association *Euphorbio ligusticae-Pinetum pinastri* Hofmann ex Pignatti 1998 *typus cons. propos.* (Pignatti 1998; Furrer and Hofmann 1969) was described for forests in the inner valleys of the Northern Apennines in the Liguria and Piedmont regions (Savona, Alessandria, Genoa, and La Spezia areas). These forests grow on nutrient-poor soils derived from ophiolitic substrates and are characterised by sub-Mediterranean serpentine-adapted species.

Since the recent Mediterranean pine forest classification revision reconsidered the syntaxonomic scheme at the alliance level (Bonari et al. 2021), there is room for the revision of lower syntaxonomic ranks (i.e. association level). Accordingly, it turns out that in some areas of Italy, particularly at the southeastern margin of the natural range of *P. pinaster* in mainland Europe, which is supposedly located in the central-southern Tyrrhenian part of Tuscany (Agostini 1968), lower syntaxonomic levels should be more thoroughly investigated. In this region, local botanists referred the heathlands with *Calluna vulgaris* and *Erica scoparia* to the association *Tuberario lignosae-Callunetum vulgaris* De Dominicis et Casini 1979, neglecting the dominant role of *P. pinaster* that physiognomically shape the forests where this association occurs (Angiolini et al. 2007). Past studies reported the dominance of *P. pinaster* in central-southern Tuscany as a result of intentional introduction in the 19th century for soil improvement and erosion control (Corti 1934; De Dominicis and Casini 1979; Piussi 1982; Mondino and Bernetti 1998; Selvi et al. 2016). Despite this, recent phytogeographical and archival studies suggest that these pine forests may have a natural (autochthonous) origin, in southern Tuscany as well as in many other areas of the Mediterranean region (Figueiral 1995; Martínez and Montero 2004; Gabellini and Saveri 2016; Caudullo et al. 2017; Bonari et al. 2021). Recent studies have also highlighted that these forests are genetically most similar to those in nearby Corsica, and to a lesser extent, to those in Liguria and southern France (Theraroz et al. 2024).

Overall, this paper aims to (i) revise *P. pinaster*-dominated communities of the Italian peninsula with special regard to central-southern Tuscany, and (ii) assess their floristic and ecological differences.

Methods

Study area

The sampling area is situated in central-southern Tuscany, south-west of the city of Siena, on the eastern side of the Colline Metallifere hilly-mountain complex, with elevations ranging from 100 to 800 m a.s.l. (Figure 1). The area falls within the catchment basin of the Farma stream, the main tributary of the Merse river. The

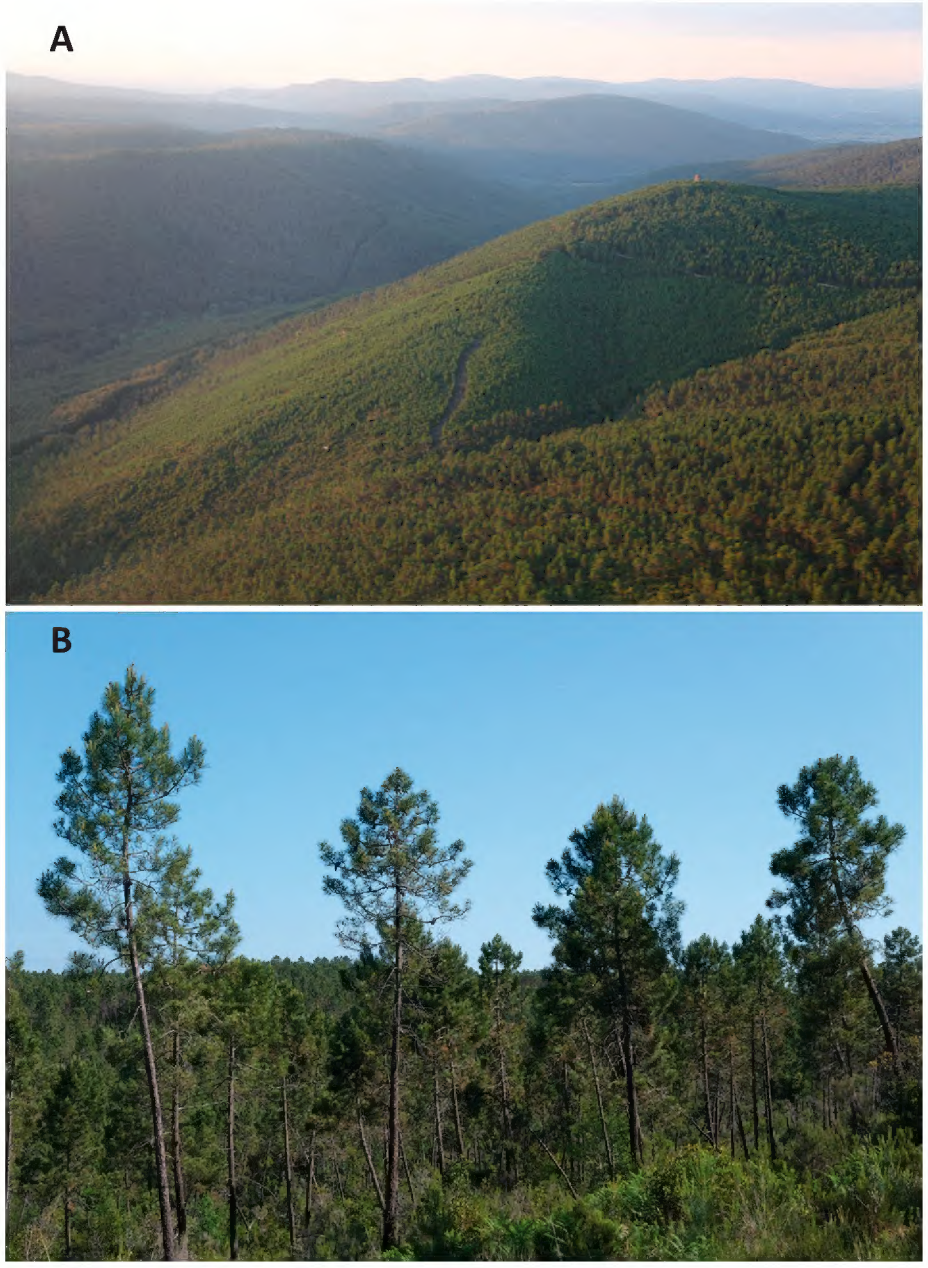

Figure 1. Aerial view (A) and ground view (B) of *Pinus pinaster* forests at their southeasternmost distribution limit in the Italian peninsula (Siena, Italy). Photo credit: G. Bonari, 2016 and 2023, respectively.

lithologies comprise siliceous rocks, mainly composed by the Verrucano Group, silty schists with varying amounts of sandstone, quartzites and anagenites – which give rise to soils of acidic nature, and limited outcrops of karstic limestone and ophiolites (Aldinucci et al. 2008; Carmignani et al. 2013). The area is influenced by a temperate macroclimate, characterised by a strong submediterraneity index, lower mesotemperate thermotype, and upper subhumid ombrotype (Pesaresi et al. 2014). The mean temperature ranges from 5 °C in January to 23.1 °C in July (Landi 2016). Precipitation is seasonal, with autumn (November-December) and winter (January-February) months having a mean of 40 mm/month and summer (July-August) months with a range of 20–40 mm/month (Landi 2016). Within the area, there are significant microclimatic differences with decreasing precipitation moving from the western side to the eastern side of the mountain chain (De Dominicis and Casini 1979), and greater temperature variation on the ridges and thermal inversions in the valley floors (Landi 2016). The study area is included in three Special Areas of Conservation (SACs) of the Natura 2000 network of protected areas (SAC IT5190006 - "Alta Val di Merse"; SAC IT51A0003 - "Val di Farma"; and SAC IT5190007 - "Basso Merse"), which are also part of four Nature Reserves ("Tocchi" Biogenetic Reserve, "Alto Merse" Nature Reserve, "Farma" Nature Reserve and "Belagaio" Nature Reserve).

The main vegetation types in the area include monospecific *P. pinaster* forests, from 8 to 20 m tall, with an understory of thermophilous evergreen shrubs and a sparse herbaceous layer. Other forests include deciduous oak forests dominated by *Quercus cerris*, *Q. petraea*, and *Castanea sativa*, and evergreen sclerophyllous forests with *Quercus ilex*. *Carpinus betulus* forests with relict stands of *Fagus sylvatica* and riparian woods with *Alnus glutinosa* and *Osmunda regalis* of the alliance *Osmundo-Alnion glutinosae* dominate the floors of the humid valleys (Landi and Angiolini 2010). Acidophilous heathlands with *Calluna vulgaris*, *Erica scoparia* and *E. arborea* are widespread in the area (Angiolini et al. 2007). The entire area remains well-preserved, with low human density concentrated in small towns and a complete absence of industrial activities. Olive groves and vineyards occur sparsely in the surroundings.

Data collection and analysis

We sampled 50 10 × 10 m original vegetation relevés subjectively placed all over the study area in May and June 2022, encompassing the major environmental local gradients (see Suppl. material 1: figure S1.1). We recorded the presence and percentage cover of the *taxa*. To compare the surveyed relevés with other *Pinus pinaster*-dominated forests of the Italian peninsula, we retrieved in total 244 published (i.e., Furrer and Hofmann 1969; De Dominicis and Casini 1979; Chiarucci and De Dominicis 1995; Bertacchi et al. 2004; Catalano 2004; Landi et al. 2009; Biondi and Vagge 2015) and unpublished relevés from the north-western part of the Italian peninsula (Liguria and Tuscany regions) from *CircumMed Forest Database* (Bonari et al. 2019b). The resulting dataset (N = 294) was then filtered keeping only relevés where *P. pinaster* had a cover value ≥ 15% and where this species cover was higher than the sum of the broadleaved tree species cover (Bonari et al. 2021), resulting in a final dataset of 251 relevés. The cover threshold of 15% was chosen as it represented a compromise that excluded open vegetation with the presence of pines, but at the same time included plots that represented forests and open pine woodlands (Bonari et al. 2021). Furthermore, our classification analysis supported this choice as it effectively delineated distinct groups. Syntaxonomic nomenclature of Mediterranean pine forests follows the EuroVegChecklist (EVC; https://www.synbiosys.alterra.nl/evc/; Mucina et al. 2016), except for the class and order ranks, which follow Bonari et al. (2021). For phytosociological nomenclature, we followed the fourth edition of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021). We identified vascular plants and their ecological and adaptive traits using the Flora of Italy and the Flora d'Italia Digitale (Pignatti et al. 2017–2019). The plant names follow Euro+Med PlantBase (Euro+Med 2024-). We also consulted FloraVeg.EU (FloraVeg.EU 2024; Chytrý et al. 2024). All the analyses were performed in the R 4.3.2 environment (R Core Team 2023).

For those relevés from the *CircumMed Forest Database* recorded with the Braun-Blanquet methodology, the cover values of species were transformed into mid-percentage values of individual grades. In all the relevés, the cover values of the same species present in different layers were combined into a single layer, accounting for the possibility of multiple layers overlapping (Tichý and Holt 2006).

We performed TWINSPAN (Hill 1979) to classify the relevés using the '*twinspan*' package (Oksanen and Hill 2023). We used five pseudospecies cut levels (0%, 2%, 5%, 10%, 20%) of species percentage cover.

Then, to explore general patterns of forest communities and to highlight changes in species composition among groups, we ran a principal coordinate analysis (PCoA) of the dataset using the '*vegan*' package (Oksanen et al. 2019). The PCoA model was based on the square-root transformed Bray-Curtis dissimilarity matrix, which was calculated on square-root transformed cover values. Based on the permutation test (p-value ≤ 0.001), we chose the best-fitted species, meaning we projected species showing a correlation coefficient >0.5 with the first two axes and superimposed them in the ordination diagram. To help the interpretation, we also mapped the latitude and longitude of the relevés for each cluster. We defined diagnostic species as those species with a phi coefficient ≥0.3, and constant species as those with a percentage frequency >20%. To compliment this, we used Ecological Indicator Values (EIVs) to better understand their ecological preferences (Pignatti et al. 2017–2019). Ecological Indicator Values inform about the adaptation of a plant species to climatic and edaphic conditions: each species is given values denoting the position at which it reaches peak abundance along environmental gradients (Diekmann 2003). A 9- or 12-point ordinal scale for each of the following parameters is used: temperature, light, soil moisture, soil nitrogen status, soil reaction (pH), continentality, and salinity – the latter two were not used since they are not informative for the vegetation type studied in this paper. To detect differences in unweighted community medians of EIVs among clusters, a Kruskall-Wallis H omnibus test, followed by post-hoc Dunn's multiple comparison test with the Holm correction method to adjust for family-wise Type I error (Holm 1979).

Finally, to investigate the adaptive characteristics of the communities of the clusters, we investigated the life forms and chorotypes spectra by plotting bar charts.

Results

The first TWINSPAN division separated two main pine forest communities, suggesting a distinction that was based on substrates. The TWINSPAN classification was cut at the second level of division, taking into account species composition, geographic distribution, type relevés, and information on their ecology gleaned from the literature (Figure 2).

The same groups can also be distinguished in the ordination PCoA diagram (Figure 3). The clusters were well separated along the two main axes. Axis 1 distinguishes pine forest communities according to a substrate gradient, while axis 2 represents a latitudinal gradient.

The distribution map of the plots is provided in Figure 4. Cluster 1 is concentrated in the eastern Ligurian area, cluster 2 is distributed in central-southern Tuscany and marginally in western Liguria (one relevé), cluster 3 is located in southern Tuscany in a small serpentine area, and cluster 4 is located over the eastern and western Liguria region.

We report an abbreviated synoptic table of diagnostic and constant species across clusters (Table 1). Cluster 1 includes mainly acidophilous species (e.g. *Castanea sativa*, *Pteridium aquilinum*, *Teucrium scorodonia*), cluster 2 encompasses evergreen acidophilous species (e.g. *Arbutus unedo*, *Calluna vulgaris*, *Erica scoparia*), cluster 3 reports a mixture of heavy-metal tolerant species (e.g. *Plantago holosteum*, *Thymus striatus*), and cluster 4 shows a mixture of grassland and garrigue species on serpentine-derived soils (e.g. *Brachypodium phoenicoides*, *Euphorbia spinosa*

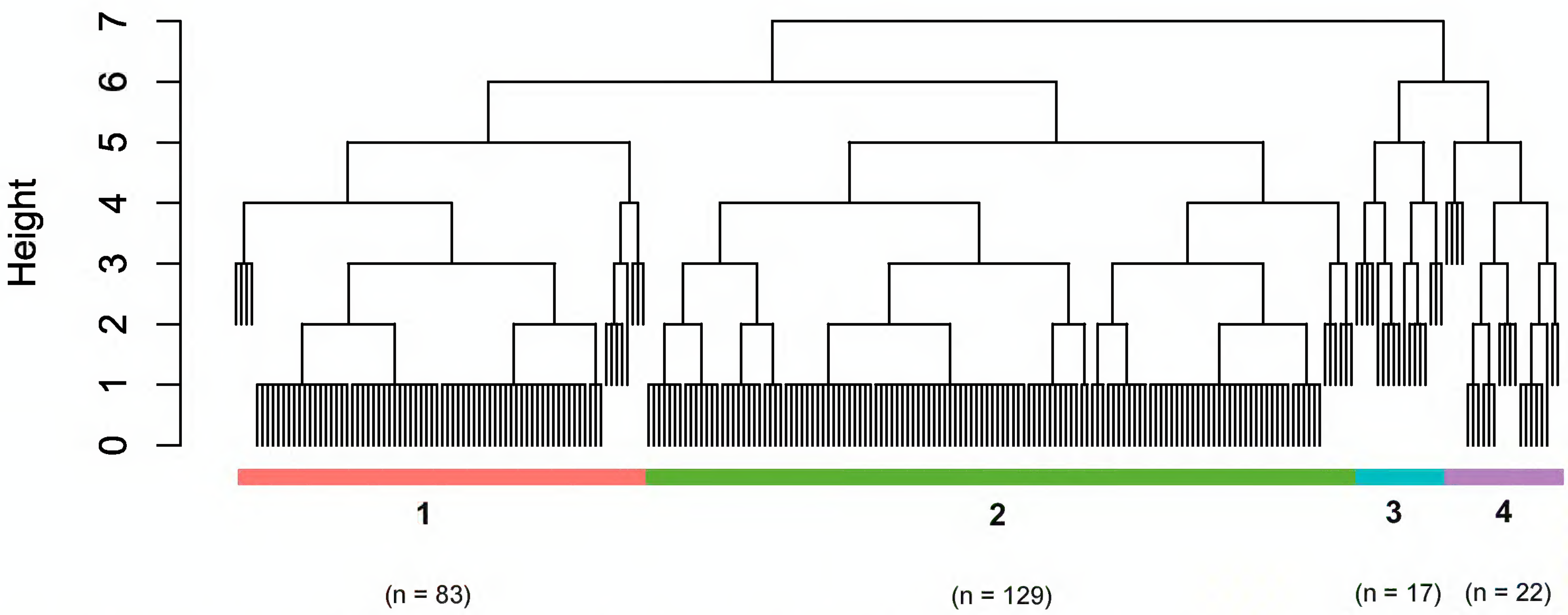

Figure 2. Dendrogram of a TWINSPAN classification based on the species composition of *Pinus pinaster* forest plots. The colours refer to: red - Cluster 1 (Eastern Liguria); green - Cluster 2 (Central-Southern Tuscany and marginally Western Liguria); light blue - Cluster 3 (Southern Tuscany); purple - Cluster 4 (Eastern and Western Liguria). The number of relevés for each cluster is specified in brackets.

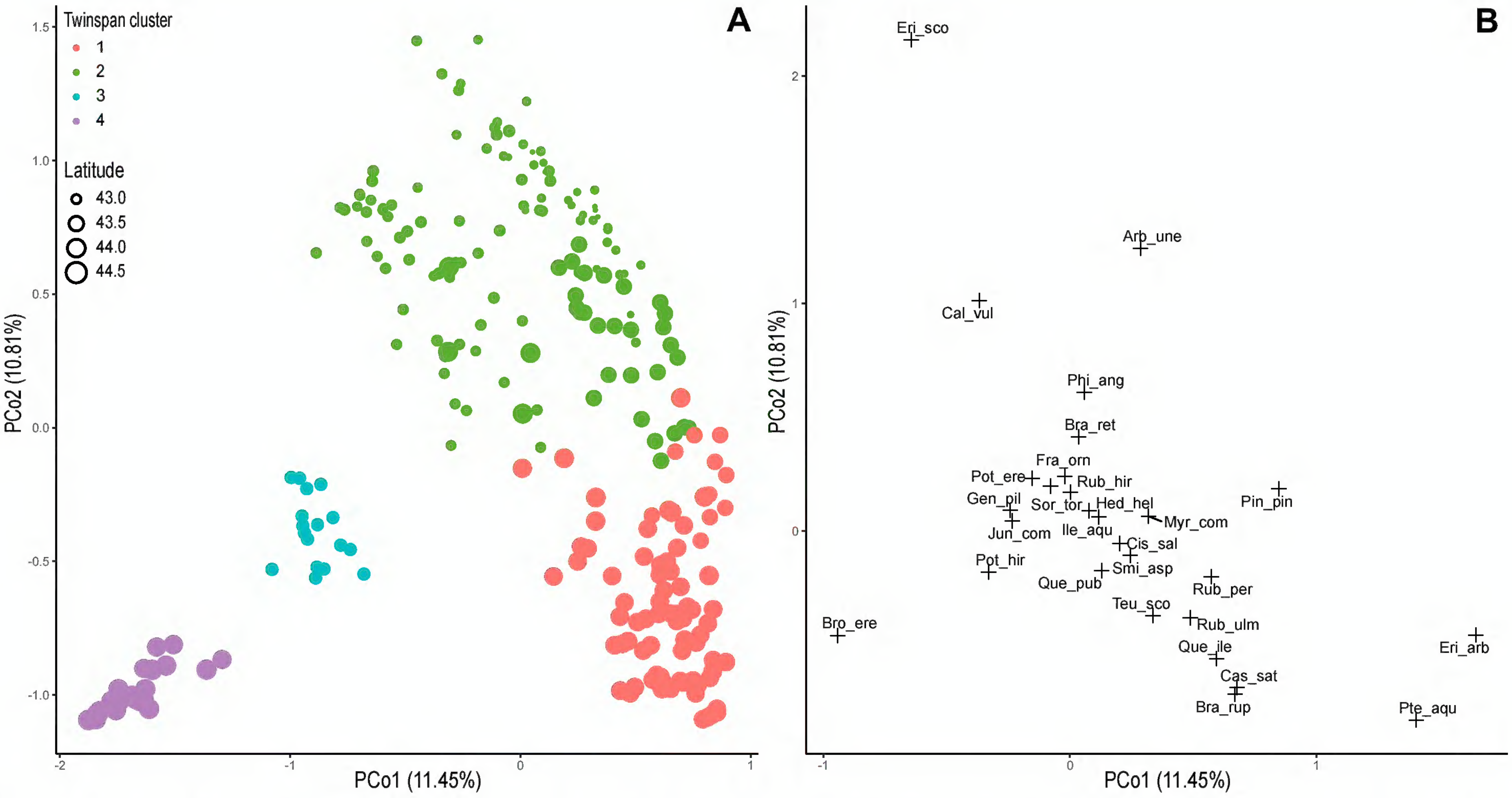

Figure 3. PCoA results showing *Pinus pinaster* forest plots in relation to latitude and clusters (A) and associated species (B). The colours refer to: red - Cluster 1 (Eastern Liguria); green - Cluster 2 (Central-Southern Tuscany and marginally Western Liguria); light blue - Cluster 3 (Southern Tuscany); purple - Cluster 4 (Eastern and Western Liguria). Species showing a correlation coefficient >0.5 with the first two axes have been superimposed to the ordination diagram (B), and are shown with a (+).

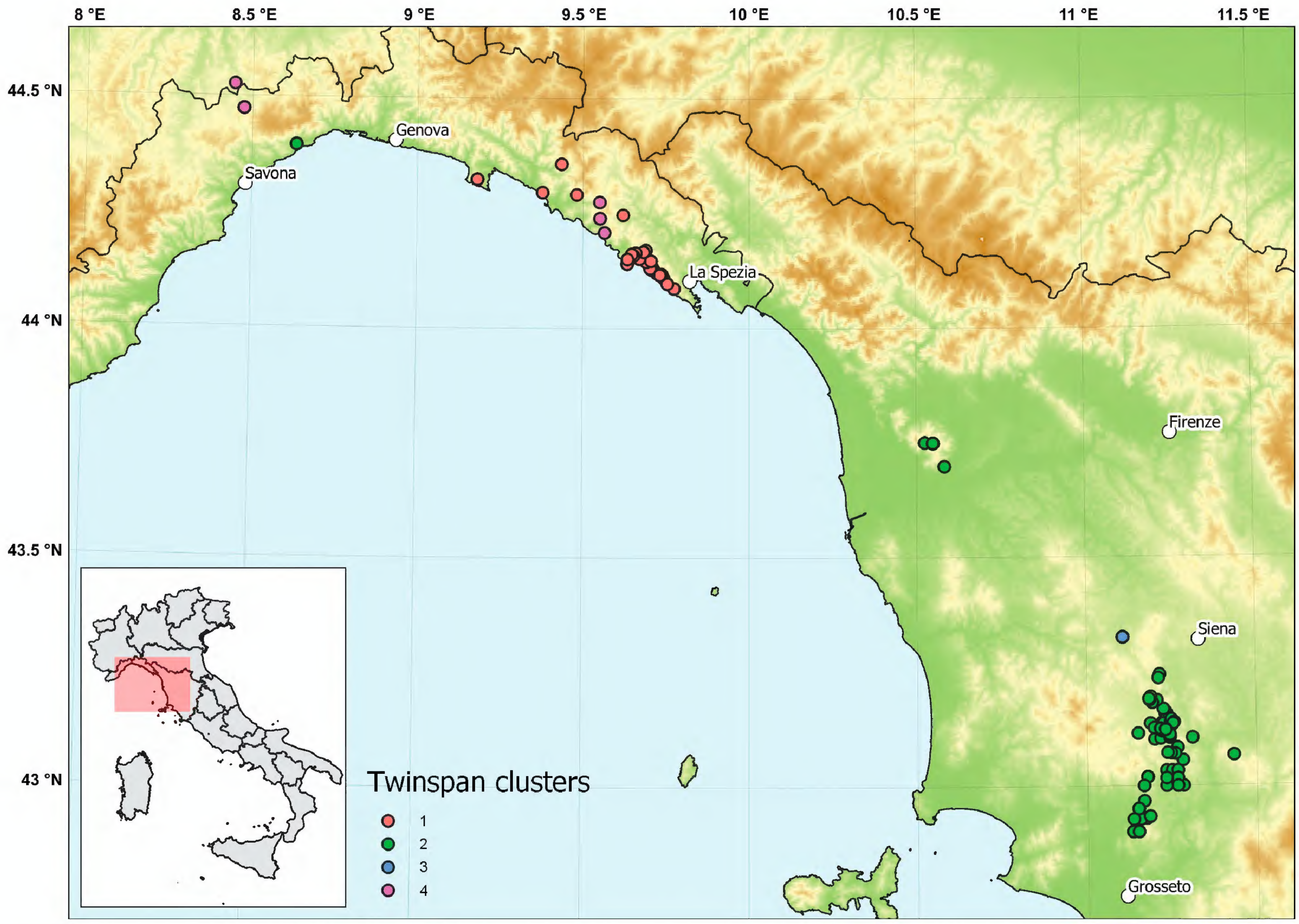

Figure 4. Map showing the distribution of the clusters in relation to the study area. The colours refer to: red - Cluster 1 (Eastern Liguria); green - Cluster 2 (Central-Southern Tuscany and marginally Western Liguria); light blue - Cluster 3 (Southern Tuscany); purple - Cluster 4 (Eastern and Western Liguria). In the upper-right box, the distribution of *Pinus pinaster* in Italy is reported (Caudullo et al. 2017).

Table 1. Abbreviated table of diagnostic and constant species of the clusters resulting from hierarchical cluster analysis (TWINSPAN). For each cluster, only species with a phi coefficient ≥0.45 and constant species with a percentage occurrence frequency >50% are shown. Species are sorted by decreasing phi coefficient for each cluster, but only the percentage frequency is shown. The frequency values >50% are indicated in grey shading. Cluster 1: Eastern Liguria; Cluster 2: Central-Southern Tuscany and marginally Western Liguria; Cluster 3: Southern Tuscany; Cluster 4: Eastern and Western Liguria. See Suppl. material 2: table S2.1 for the full synoptic table and the complete list of species.

Species	**Cluster 1** (n = 83)	**Cluster 2** (n = 129)	**Cluster 3** (n = 17)	**Cluster 4** (n = 22)
Teucrium scorodonia	70	3	.	.
Brachypodium rupestre	67	9	24	.
Pteridium aquilinum	86	41	.	.
Quercus ilex	78	31	18	.
Castanea sativa	69	22	.	9
Rubus ulmifolius	73	30	24	.
Erica scoparia	1	80	76	.
Calluna vulgaris	4	70	.	14
Arbutus unedo	48	88	.	.
Thymus striatus	.	.	100	.
Plantago holosteum	.	.	94	.
Convolvulus cantabrica	.	.	88	5
Festuca robustifolia	.	.	82	.
Genista januensis	4	1	100	.
Koeleria splendens	.	.	76	.
Galium corrudifolium	.	.	71	.
Sanguisorba minor subsp. *balearica*	.	.	65	.
Galatella linosyris	.	.	59	.
Knautia arvensis	.	.	59	.
Stipa etrusca	.	.	53	.
Juniperus oxycedrus	5	3	82	.
Centaurea aplolepa	1	.	100	91
Bromopsis erecta	.	2	94	86
Festuca ovina aggr.	1	.	94	95
Potentilla hirta	.	.	76	91
Brachypodium phoenicoides	.	.	.	100
Plantago maritima subsp. *serpentina*	.	.	.	91
Scabiosa pyrenaica	.	.	.	91
Teucrium montanum	1	.	.	91
Galium purpureum	.	.	.	86
Euphorbia spinosa subsp. *ligustica*	1	2	.	100
Satureja montana	1	1	.	91
Asperula aristata	.	.	.	82
Helictochloa pratensis	.	.	.	82
Scorzonera austriaca	.	.	.	82
Thymus serpyllum	.	.	.	77
Trinia glauca	.	.	.	77
Pilosella piloselloides	.	.	6	77
Carex humilis	2	2	.	86
Sorbus aria	.	2	.	77
Peucedanum oreoselinum	.	2	.	68
Peucedanum cervaria	4	1	.	59
Lotus corniculatus	.	2	6	55
Anthericum liliago	1	11	6	64

subsp. *ligustica*, *Plantago maritima* subsp. *serpentina*, *Thymus serpyllum*). See Suppl. material 2 for the full synoptic table and the complete list of species.

The analysis of Ecological Indicator Values helped to further characterise the ecology of each cluster (Figure 5). Cluster 1 had the highest mean value of soil moisture, temperature (with no significant differences to cluster 2) and the lowest mean value for light (significantly different from clusters 2, 3, and 4). Cluster 2 significantly differed from clusters 3 and 4, having the lowest mean value for soil

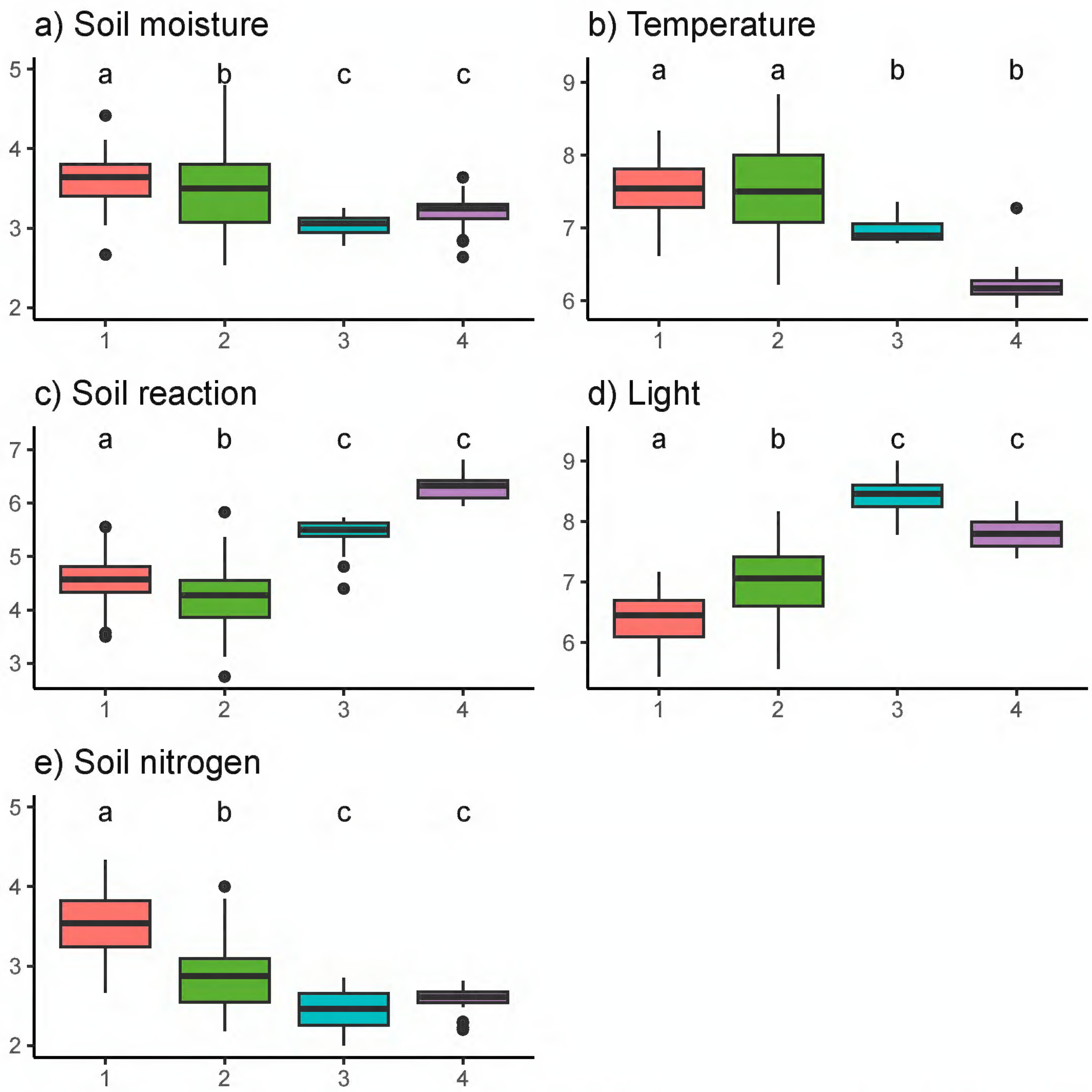

Figure 5. Boxplots of unweighted community means of Ecological Indicator Values showing the results of the post-hoc Dunn's multiple comparison test with Holm correction. The results of pairwise comparisons are indicated using Compact Letter Display method, where different letters between two clusters indicate a statistically significant difference of the test, with $p < 0.05$. The colours refer to: red - Cluster 1 (Eastern Liguria); green - Cluster 2 (Central-Southern Tuscany and marginally Western Liguria); light blue - Cluster 3 (Southern Tuscany); purple - Cluster 4 (Eastern and Western Liguria).

reaction, which indicates an acidophilous plant community. Cluster 3 had the lowest mean value for soil moisture (indicating a markedly xerothermic plant community) and soil nitrogen (with no significant differences to cluster 4) and the highest mean value for light, whereas cluster 4 showed the lowest temperature and the highest soil reaction.

Analysis of life forms (Suppl. material 1: figure S1.2A) showed how the clusters differentiate particularly in the share of phanerophytes and hemicryptophytes, with cluster 2 having the highest percentage of phanerophytes and the lowest of hemicryptophytes. However, the clusters did not differentiate clearly in terms of chorotypes, apart from their share of endemic species to Italy, which was particularly high in cluster 3 (Suppl. material 1: figure S1.2B).

Discussion

The presented analytical comparison of Ligurian-Tuscan *Pinus pinaster* forests highlights the floristic-vegetational diversity of the investigated communities. These forests thrive in diverse edaphic conditions, occurring on both siliceous and ultramafic substrates, and are distributed along a broad climatic gradient encompassing Temperate and Mediterranean areas. Results indicate floristic and ecological similarity of the studied community in central-southern Tuscany to the association *Erico scopariae-Pinetum pinastri* described by Biondi and Vagge (2015) in eastern Liguria and northern Tuscany. This vegetation unit is the type association of the alliance *Genisto pilosae-Pinion pinastri*. The occurrence of taxa such as *Erica arborea*, *E. scoparia*, *Calluna vulgaris*, *Cistus salviifolius*, *Fraxinus ornus*, and *Genista pilosa* confirms that this community belongs to the alliance *Genisto pilosae-Pinion pinastri*. This alliance is classified by the EVC (Mucina et al. 2016) to the order *Quercetalia ilicis* and to the class *Quercetea ilicis*. However, the results of Bonari et al. (2021) supported moving Mediterranean pine forests to the order *Pinetalia halepensis* and class *Pinetea halepensis* based on structure, physiognomy, and diagnostic species. The number of diagnostic species of the class *Pinetea halepensis* is lower if compared to the class *Quercetea ilicis*, but the decision of Bonari et al. (2021) to move low-elevation Mediterranean pine forests to a separate class is based, among other reasons, on diagnostic species analysis (see table 3 in Bonari et al. 2021). Thus, in this paper,

we adopted the most recent classification proposed by Bonari et al. (2021) for the nomenclature and positioning of the higher syntaxa.

A significant difference in floristic composition exists between the forests under investigation and the association *Erico arboreae-Pinetum pinastri* of northern Tuscany. Both are characterised by a group of species serving as vicariants (e.g., *Erica scoparia* vs. *E. arborea*, *Genista pilosa* vs. *G. germanica*, *Lonicera implexa* vs. *L. etrusca*, *Brachypodium retusum* vs. *B. rupestre*, *Rubus hirtus* vs. *R. ulmifolius*). In the forests of central-southern Tuscany, the understory is richer in shrubs and chamaephytes, featuring a diverse array of narrow-leaved xerophytes. However, geophytes and therophytes are scarce, even though both vegetation types are species-poor. Since the forest canopy is relatively open, the presence of light-demanding taxa is common (e.g., *Danthonia decumbens*, *Potentilla erecta*, *Serratula tinctoria*, *Tuberaria lignosa*), which is consistent with findings in other Mediterranean pine forests (Bonari et al. 2017, 2018). Furthermore, this *P. pinaster* forest community is closely associated, both spatially and dynamically, with acidophilous *Erica* spp. and *Calluna vulgaris* dominated heathland. This community has been previously classified in the association *Tuberario lignosae-Callunetum vulgaris* (De Dominicis and Casini 1979). The pine forest-relatable scrub vegetation is relevant in this context as a heath scrub transitions into pine forest as pine density increases.

Central-southern Tuscany forests stand out as they host a significant number of Stenomediterranean species, including a notable group with a Eurimediterranean distribution (e.g. *Fraxinus ornus*, *Rubus ulmifolius*, *Sorbus domestica*). Nevertheless, the percentage of European, Eurasian, and Boreal taxa (e.g., *Calluna vulgaris*, *Danthonia decumbens*, *Molinia arundinacea*, *Potentilla erecta*) suggests that there is a substantial influence from the Euro-Siberian region. In particular, the occurrence of *Calluna vulgaris* holds great phytogeographic interest as it marks the southern boundary of its distribution in Italy (Bernetti 1987). In addition, the unique combination of a hyperoceanic climate and dystric cambisols-ferric podzols featuring highly acidic raw humus in this part of Tuscany supports the occurrence of various Atlantic and Mediterranean-Atlantic species, such as *Erica scoparia*, *Genista pilosa*, and *Teucrium scorodonia* (Angiolini et al. 2007). Forests in central-southern Tuscany show clear distinctions from those with similar physiognomy found in Sardinia, where they are classified under the association *Arbuto unedonis-Pinetum pinastri*. While both regions exhibit dominance of sclerophyllous shrubs and vines, along with a sparse herbaceous layer, they differ in terms of a specific set of diagnostic species that are practically absent in the Italian Peninsula (Calvia et al. 2022a).

According to our analysis, the association *Buxo sempervirentis-Pinetum pinastri* seems to be floristically similar to the species composition of the association *Erico arboreae-Pinetum pinastri*. However, we preferred not to synonymize the two associations since the latter was described by Biondi and Vagge (2015) using very few relevés from a small area with siliceous bedrock in the Chiavari inland of central Liguria. We, therefore, preferred to consider this association as doubtful. Further studies are needed to elucidate the syntaxonomic status of this vegetation unit.

Our analysis confirms the floristic autonomy of forests found on ophiolitic substrates in the Liguria region. Along with the occurrence of shrubs like *Juniperus communis*, *Amelanchier ovalis* and *Sorbus aria*, and a xerophilous herbaceous layer featuring, e.g., *Brachypodium phoenicoides*, *Bromopsis erecta*, *Festuca ovina* aggr., and *Teucrium montanum*, several species characteristic of ophiolitic substrates are found, including *Centaurea aplolepa*, *Euphorbia spinosa* subsp. *ligustica*, *Cherleria laricifolia* subsp. *ophiolitica*, *Plantago maritima* subsp. *serpentina* and *Thymus serpyllum*. Hofmann (1960) was the first who provided a detailed description of this forest type from the Deiva State Forest (Savona) under the names "*Euphorbietum spinosae pinetosum pinastri*" ("phytosociological name") and "*Euforbieto-Pinetum*" ("sylvicultural name"). Both names are invalid because they were proposed as provisional (ICPN, Art. 3b), without relevés or a synoptic table with clearly defined frequency classes (Arts. 2b, 7). The subassociation name would also be invalid according to Art. 4a. Some years later, Furrer and Hofmann (1969) validly published the "*Euphorbietum spinosae-ligusticae*" (recte: *Euphorbietum ligusticae*) with a table of 36 relevés from Liguria (Savona, Genoa, Alessandria, and La Spezia). The name is legitimate according to Art. 29b because in all relevés (excepting relevé 8, dominated by *P. pinaster*) the herb and low shrub cover is higher than the cover of shrubs and trees. Indeed, *Euphorbia ligustica* dominates over *Pinus pinaster* in 23 relevés and co-dominates with it in 9 relevés; *Pinus* dominates over *Euphorbia* in 4 relevés, but in two of them the dominant plant is a grass species. Later on, Pignatti (1998: 437, 642) accepted the name "*Euphorbio ligusticae-Pinetum pinastri* Furrer & Hofmann (1960)" citing the "*Euphorbietum spinosae-ligusticae* Furrer & Hofmann (1960)" as a synonym. Despite some inconsistencies in the references that can be interpreted as bibliographical errors (Art. 2b Note 3), it is clear that Pignatti's name "*Euphorbio ligusticae-Pinetum pinastri* Hofmann ex Pignatti 1998" is an incidental later validation of one of Hofmann's names and a superfluous name (Art. 29c) for the *Euphorbietum ligusticae* Furrer et Hofmann 1969. In fact, Pignatti provides a reference to the table of Furrer and Hofmann (1969) excluding four relevés from Genoa in which pine is absent. Pignatti's name has been rarely used, but is a good name for the *P. pinaster* forests on ophiolites from Liguria belonging to the *Genisto pilosae-Pinion pinastri*. Therefore, we propose to conserve the *Euphorbio ligusticae-Pinetum pinastri* Hofmann ex Pignatti 1998 *typus cons. propos.* with the relevé 8 (16th in the table; *Pinus pinaster* cover: 4; *Euphorbia ligustica*: 2) of the table in Furrer and Hofmann (1969) as *typus conservandum* according to Art. 53 of the ICPN. This proposal will be submitted to the CCCN for approval

by the GPN Assembly. To fix the syntaxonomic concept of the *Euphorbietum ligusticae* Furrer et Hofmann 1969, we designate as *lectotypus hoc loco* the relevé 12 (3rd in the table; *P. pinaster* cover: 1; *Euphorbia ligustica*: 3) of the table in Furrer and Hofmann (1969). Both relevés come from Savona area, considered by the authors as the most representative of the floristic composition of the association. The *Euphorbietum ligusticae* is currently included in the alliance of scrub vegetation on serpentines *Alyssion bertolonii* E. Pignatti et Pignatti 1977 (Vagge 1997; Mucina et al. 2016; Terzi et al. 2022).

Our classification includes an informal group comprising of pine forest plantations established on ultramafic bedrock in southern Tuscany (Chiarucci 2004). In line with Bonari et al. (2021), we preferred not to describe a formal syntaxon for pine plantations in areas where the pines are clearly planted.

From a habitat perspective, the studied pine forest communities were not included in Annex I of the 92/43/EEC Habitats Directive. On the one hand, this exclusion is due to the extensive use of *P. pinaster* for past reforestation in the surrounding areas, making it difficult to distinguish native sites from artificially established ones. On the other hand, old-established plantations of native pine species can develop an understory of natural species composition that makes these forest communities valuable in terms of nature conservation (Bonari et al. 2017, 2019a, 2020). We suggest, therefore, to attribute these communities to the habitat type 9540 "Mediterranean pine forests with endemic Mesogean pines" included in Annex I of the 92/43/EEC Habitats Directive, and specifically to the subtype no. 42.823 "Franco-Italian Mesogean pine forests: *Pinus pinaster* forests of siliceous lower meso-Mediterranean areas of Provence, of marls and limestones of the upper meso-Mediterranean level of the Maritime Alps and the Ligurian Alps, and of mostly siliceous or clayey soils of the hills of Liguria and Tuscany" (Biondi et al. 2010). This habitat is also featured as "T3A Mediterranean lowland to submontane *Pinus* forests" according to the EUNIS Habitat Classification (Chytrý et al. 2020). These classification systems include old-established plantations within the natural distribution of the pine. We support the extension of the natural distribution of *P. pinaster* into central-southern Tuscany, *sensu* Caudullo et al. (2017), which is also aligned with the observations of Agostini (1968). The presence of these forests in Tuscany is indeed due to the combination of favourable climatic and edaphic conditions that allow this species to thrive in this region. Additionally, the extensive distribution of these forests, though undoubtedly impacted by the establishment of plantations at places (Selvi et al. 2016), can be partly also attributed to the pioneering nature of the pine, which has exhibited a trend of expansion and recovery of natural conditions over the last few decades in southern Europe, including Liguria and Tuscany regions (De Dominicis and Casini 1979; Arrigoni 1997; Gabellini and De Dominicis 2003; Wyse et al. 2019; Santoro et al. 2021; Calvia et al. 2022b).

Conclusions

Our study has expanded the floristic and ecological knowledge of *Pinus pinaster* forests at the southeasternmost margin of their European mainland distribution range and has contributed to their classification by proposing an updated syntaxonomic scheme. We extended the occurrence of the alliance *Genisto pilosae-Pinion pinastri* (class *Pinetea halepensis*) to central-southern Tuscany, beyond the Ligurian-Provençal seaboard. Based on ecological characteristics, diagnostic species, type relevés, and information gleaned from existing literature, we confirmed the associations *Erico arboreae-Pinetum pinastri* and *Erico scopariae-Pinetum pinastri*, distributed from eastern Liguria to southern Tuscany on siliceous soil conditions. Importantly, we identified a syntaxonomic placement for the forests of central-southern Tuscany, which previously lacked classification at the association level, attributing them to the association *Erico scopariae-Pinetum pinastri*. Additionally, we identified two communities on ultramafic substrate: one confined to central Liguria, proposed in our study as association *Euphorbio ligusticae-Pinetum pinastri*, for which we suggest conserving the association name, and another one found in central Tuscany and consisting of introduced plantations. The results of this study underscore the importance of conserving the central-southern Tuscany *P. pinaster* forests, not only because the dominant pine species is situated at the southeasternmost boundary of its distribution on the Italian peninsula, but also due to the presence of species with phytogeographical significance in the forest understory.

Syntaxonomic scheme

Class *PINETEA HALEPENSIS* Bonari et Chytrý in Bonari et al. 2021

- Order *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014
  - Alliance *Genisto pilosae-Pinion pinastri* Biondi et Vagge 2015
    - Association *Erico arboreae-Pinetum pinastri* Biondi et Vagge 2015 [Cluster 1]
    - Association *Erico scopariae-Pinetum pinastri* Biondi et Vagge 2015 [Cluster 2]
      - *Pinus pinaster* secondary plantations on serpentine of southern Tuscany (informal group) [Cluster 3]
    - Association *Euphorbio ligusticae-Pinetum pinastri* Hofmann ex Pignatti 1998 *typus cons. propos.* [Cluster 4]
    - Association ? *Buxo sempervirentis-Pinetum pinastri* Biondi et Vagge 2015

The question mark "?" refers to the doubtful syntaxonomic status of this vegetation unit.

Data availability

Relevés of this article are available upon request through the *CircumMed Forest Database* (Global Index of Vegetation-Plot Databases, ID: EU-00026).

Author contributions

G.B. planned the research; D.C. and M.M.V. conducted the field sampling with support of M.L.; D.C., M.M.V., M.L., and G.B. identified plant specimens; M.M.V. and K.C. performed the statistical analyses; D.C. and M.M.V. led the writing and review with major contributions of G.B. All authors critically revised the manuscript and approved the final and revised version.

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E-mail and ORCID

Dario Ciaramella (Corresponding author, dario.ciaramella93@gmail.com), ORCID: https://orcid.org/0000-0003-3646-0546
Martina Marei Viti (martina.viti@idiv.de), ORCID: https://orcid.org/0000-0002-9392-9948
Marco Landi (marcolandi.siena@gmail.com), ORCID: https://orcid.org/0000-0002-5525-0758
Kryštof Chytrý (krystof.chytry@gmail.com), ORCID: https://orcid.org/0000-0003-4113-6564
Claudia Angiolini (angiolini@unisi.it), ORCID: https://orcid.org/0000-0002-9054-9480
Gianmaria Bonari (gianmaria.bonari@unisi.it), ORCID: https://orcid.org/0000-0002-5574-6067

Supplementary material

Supplementary material 1
Distribution of the relevés, life form and chorotype spectra of individual clusters (.docx file)
Link: https://doi.org/10.3897/VCS.118023.suppl1

Supplementary material 2
Synoptic table with percentage frequency and phi coefficient for each species in the clusters (.docx file)
Link: https://doi.org/10.3897/VCS.118023.suppl2